Simulating leaf net CO_2 assimilation rate of C_3 & C_4 plants and its response to environmental factors

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Abstract: Basic structure and algorithm of leaf mechanism photosynthesis model were described in first part of this study based on former researcher results. Then, considering some environmental factors influencing on leaf photosynthesis, three numerical sensitivity experiments were carried out. We simulated the single leaf net CO_2 assimilation, which acts as a function of different light, carbon dioxide and temperature conditions. The relationships between leaf net photosynthetic rate of C_3 and C_4 plant with CO_2 concentration intercellular, leaf temperature, and photosynthetic active radiation (PAR) were presented, respectively. The results show the numerical experiment may indicate the main characteristic of plant photosynthesis in C_3 and C_4 plant, and further can be used to integrate with the regional climate model and act as land surface process scheme, and better understand the interaction between vegetation and atmosphere.

Key words: Photosynthesis model; Net CO_2 assimilation rate; C_3 and C_4 plants; Numerical simulation
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Introduction [1]

It is well recognized that the global climate is becoming warmer and warmer owing to increased emission of greenhouse gases affected by human activities. The better method of predicting future climate trend is to use regional and global climate model. Recent years, a series of such kinds models have been developed to describe the interaction between the biosphere to atmosphere, and several of land surface interaction complex process schemes have been incorporated into regional or global climate models (Dickinson *et al.*, 1986; Sellers *et al.*, 1986, 1992, 1996; Xue *et al.* 1991; Foley *et al*, 1996). As we know, the land surface process in regional climatic model (RCM) employed in eco-physiology are designed to describe the basic photosynthesis process at the leaf, canopy and regional levels together with the stomatal conductance, vegetation transpiration, CO_2 flux change within leaf. Representation of CO_2 exchanges at the surface-atmosphere interface is an important challenge for assessing the impact of climatic change on the surface energy and water budget, and it has been suggested that the exchange of water vapor and CO_2 between vegetation canopies and the atmosphere is strongly controlled by the physiological processes governing photosynthesis and stomata conductance. Thus, developing models to estimate photosynthesis is certainty.

The purpose of current study is to simulate the response of photosynthesis of C_3 & C_4 pathway plants to environmental affecting elements based on former researcher schemes; additionally, is to understand the realistic photosynthesis process of difference photosynthesis pathway in vegetation. Furthermore, to develop a more realistic mechanize photosynthesis scheme for integrating RCM.

Three pathways of plant photosynthesis

Generally, based on the photosynthesis pathway, the natural flora can be divided into three categories (Monson *et al.* 1989), namely C_3 plant (by all trees and many herbs, CO_2 assimilation through reductive pentose phosphate cycle), C_4 plant (tropical herbs and warm grasses; 20 family; >12 000 species, CO_2 assimilation through PEP carboxylase), and CAM (crassulacean acid metabolism) plant (carnification plant; 26 family; >500 species). Table1 lists the main photosynthesis characteristics of C_3, C_4 and CAM plants. In present study, numerical algorithm will be adopted to approach some important photosynthetic characteristics of C_3 and C_4 plants.

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Table 1. C_3, C_4 and CAM plants photosynthesis and other eco-physiological characteristics

Characteristics	C_3 plant	C_4 plant	CAM
First step, Catalytic Reaction Fixed CO_2	Rubisco E	Rubisco E	Rubisco E
CO_2 immobilization enzyme	RuBP E	PEP carbonlase RuBP E	PEP E RuBP E
Representative plant	Wheat (crop), Pine (tree)	Corn (crop), Millet (cereal)	Cactus (shrub)
Leaf structure	Bundle-sheath (undeveloped	Bundle-sheath (developed)	
P_{max} ($mgCO_2 \cdot dm^{-2} \cdot h^{-1}$)	Low (15-40)	High (35-80)	Low (1-4)
CO_2 compensation point ($mg \cdot kg^{-1}$)	High (40-70)	Low (0-10)	Dark period (0-5) 24-h (0-200)
Light respiration	High	Low	Low
Light saturation point	Low (=1/4-1/2 R_{max})	High (above R_{max})	Unfixed
Suitable temperature of Photosynthesis	Low (15-25)	High (30-47)	-35
Suitable temperature of growing	Low	High	Widely
Resistance to arid climate	Weak	Strong	Changed
NPP ($g \cdot m^{-2} \cdot d^{-1}$)	Low (19.5± 3.9)	High (30.3±13.8)	Changed
NPP ($t \cdot hm^{-2} \cdot a^{-1}$)	Low (22.0±3.3)	High (38.6±16.9)	Changed
Water demand (g water/g dry-matter)	Large (450-950)	Small (250-350)	Very small (50-55)
Increasing of dry-matter /Doubling CO_2	high (>20%)	Low (<10%)	Unfixed

The leaf photosynthesis scheme

Modeling method

After 1980s, some mechanism photosynthesis simulating models have been set up and developed. The significant progress was Farquhar (1980) and Collatz (1990,1991) works. In their models, the photosynthetic rate (*A*) is a function of PAR, leaf temperature, CO2 flux within the leaf, and the Rubisco enzyme capacity for photosynthesis (Sellers *et al.* 1996a). In both cases the rate of gross leaf photosynthesis, *A*, is calculated in terms of three potentially limiting factors. In this paper, the term *A* of C_3 & C_4 plants are similarly modeled as the minimum of three potential capacities, be expresses as

$$A \le \min\,(w_c, w_e, w_s) \tag{1}$$

where, *A* is gross Leaf photosynthetic rate ($mol \cdot m^{-2} \cdot s^{-1}$); w_c is represents the rate of gross photosynthesis when the leaf photosynthetic enzyme (Rubisco of leaf enzyme) was limited; w_e is light- limited rate of gross assimilated rate ($mol \cdot m^{-2} \cdot s^{-1}$); w_s is the limitation associated with export of the photosynthetic products (for C_3 vegetation), or PEP-Carboxylase (for C_4 plant) limitation on photosynthesis ($mol \cdot m^{-2} \cdot s^{-1}$).

For the physiological limit of photosynthetic enzyme on assimilation rate, ω_c can be written as:
for C_3 plant

$$w_c = V_m\left[\frac{C_i - \Gamma^*}{C_i + K_c(1 + O_2 / K_0)}\right] \tag{2}$$

and for C_4 plant

$$w_c = V_m \tag{3}$$

where, w_c is Rubisco-limited rate of assimilation ($mol \cdot m^{-2} \cdot s^{-1}$); V_m refers to maximum rate of catalytic capacity of Rubisco ($mol \cdot m^{-2} \cdot s^{-1}$) at T_c; C_i is partial pressure of CO_2 in leaf interior(Pa); O_2 is partial pressure of O_2 in leaf interior (Pa); Γ^* is CO_2 compensation point (Pa) = $0.5O_2/S$; S is Rubisco specificity for CO_2 relative to O_2 (=$2600^*0.57^{Q_t}$); K_c is Michaelis-Mnten constant for CO_2 (Pa), and its value is equal to 30×2.1^{Q_t}; K_o is inhibition constant for O_2(Pa), and its value is $30\,000\times1.2^{Q_t}$, where Q_t is Q_{10} temperature coefficient, equal to $0.1\times(T_c-25)$, T_c is the leaf temperature (°C).

For C_3 plant, the term V_m is given by

$$V_m = \frac{V_{\max} Q_t}{\{1 + \exp[0.3(T_c - 38)]\}} \tag{4}$$

and for C_4 plant, it is given by

$$V_m = \frac{V_{\max} Q_t}{\{1 + \exp[0.3(T_c - 40)]\}\{1 + \exp[0.2(5 - T_c)]\}} \tag{5}$$

where, V_{max} is maximum leaf catalytic capacity of Rubisco at 25°C, the values V_{max} were given by 1×10^{-4} ($mol \cdot m^{-2} \cdot s^{-1}$) for C_3 broadleaf deciduous tree and 3×10^{-5} ($mol \cdot m^{-2} \cdot s^{-1}$) for C_4 grass (Sellers *et al.* 1996b).

The light-limited rate of assimilation w_e is given by (Foley *et al.* 1996):

$$w_e = 0.068 I_{PAR}[\frac{c_i - \Gamma^*}{c_i + 2\Gamma^*}] \quad \text{for } C_3 \text{ plant} \tag{6}$$

$$w_e = 0.0332 I_{PAR} \quad \text{for } C_4 \text{ plant} \quad (7)$$

where, I_{PAR} is the incident PAR on the leaf ($mol{\cdot}m^{-2}{\cdot}s^{-1}$), and its value depends on the assumed quantum efficiency for CO_2 uptake and the leaf scattering coefficient for PAR. In this study, it can be written the PAR multiplies an absorbed factor by 0.86 (Collatz *et al.* 1991).

A third limiting rate has been defined for C_3 and C_4 photosynthesis by Collatz *et al.* (1991, 1992), respectively, w_s is viewed as the capacity for the export or utilization of the products of photo synthesis in the case of C_3 and as the CO_2-limited capacity for C_4 photosynthesis.

$$w_s = 0.5\ V_m \quad \text{for } C_3 \text{ plant} \quad (8)$$

$$w_s = 2{\times}10^4\ V_m\, c_i/p^* \quad \text{for } C_4 \text{ plant} \quad (9)$$

where, p^* is atmospheric pressure (Pa).

The actual rate of gross photosynthesis, A, is calculated as the smoothed minimum of above three limiting rates:

$$\begin{aligned} \beta_1 w_p^2 - w_p(w_c + w_e) + w_e w_c &= 0 \\ \beta_2 P^2 - P(w_p + w_s) + w_p w_s &= 0 \end{aligned} \quad (10)$$

where, β_1, β_2 is coupling coefficients, w_p is smoothed mimmum of w_c and w_e ($mol{\cdot}m^{-2}{\cdot}s^{-1}$).

The net assimilation A_n, is then given by

$$A_n = A - R_d \quad (11)$$

where, R_d is leaf respiration rate($mol{\cdot}m^{-2}{\cdot}s^{-1}$), Collatz *et al.* (1991, 1992) scaled R_d to the leaf carboxylase Content by

$$R_d = f_d V_m \quad (12)$$

where, f_d = 0.015 for C_3 plant, and f_d = 0.025 for C_4 plant.

The numerical experiments and some results

In this study, two plant types were selected as experimental plant species, the temperate deciduous broadleaf tree (C_3 plant), located in north part of Changjiang River, and maize (C_4 plant), which is grown in North China Plain. Some experiments testing were performed via considering the some factors influencing on leaf photosynthesis. Here, we consider three kind of effect situation on photosynthetic rate. One is the dependence of leaf photosynthesis on Photosynthesis Active Radiation (PAR), second is the relationship between leaf photosynthesis and CO_2 concentration intercellular, third is the relationship between leaf photosynthesis and leaf temperature.

We simulated the net CO_2 Assimilation (A_n) in leaf level, the model at the leaf level can also be used to modeling A_n in the larger scales by scaling up. A_n response of C_3 & C_4 plants to PAR, leaf temperature, CO_2 flux within leaf for has been addressed. Fig. 1 shows the dependence of A_n in leaf level on PAR, reflects that the C_4 light saturation points is obviously higher than that of C_3 plant.

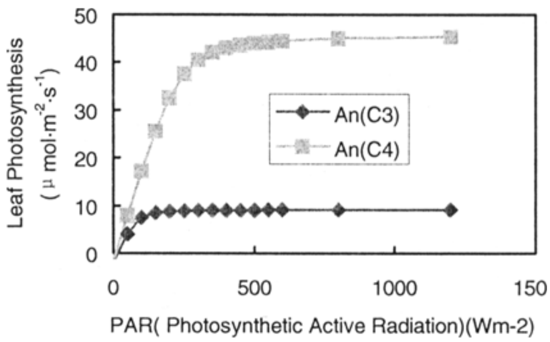

Fig.1 The relationship between leaf A_n and PAR for C_3 and C_4 plants

Fig. 2 presents the relationship between A_n and leaf temperature. In X-axis, before 20°C, with leaf temperature increases, the increasing trend of C_3 plant A_n is higher than that of C_4 plant, however, after 20°C, there is a significant increasing of A_n for C_4 plant.

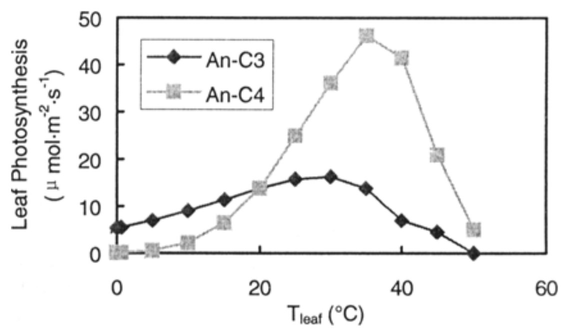

Fig.2 The relationship between leaf A_n and leaf temperature for C_3 and C_4 plants

Anyway the maximum values of A_n (C_4 plant) nearly against 36°C. But in case of C_3 plant, the leaf temperature just less than 30°C when A_n increases its peak. The result implies a better elucidation for C_4 plant originated from tropic zone, to some extant, also reflects the light saturation point of C_3 plant is less than that of C_4 plant (Harold *et al.* 1978).

Fig. 3 & Fig 4 show the relationship between A_n and C_i about C_3 and C_4 plants. Owing to CO_2 compensation point of C_3 plant is higher than that of C_4 plant, so the Fig. 3 presents there is a linear positive correlation between A_n and C_i. Nerveless, in Fig.4, A_n of C_4 plant is close to saturation with the C_i increasing. This result also reveals the increasing of dry-matter of

C_3 plant is higher than that of C_4 plant under CO_2 doubling.

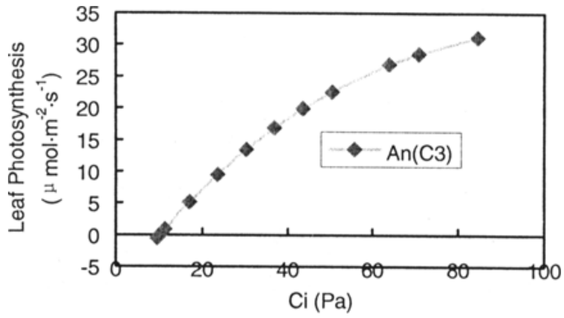

Fig. 3 The relationship between net leaf A_n and C_i for C_3 plant

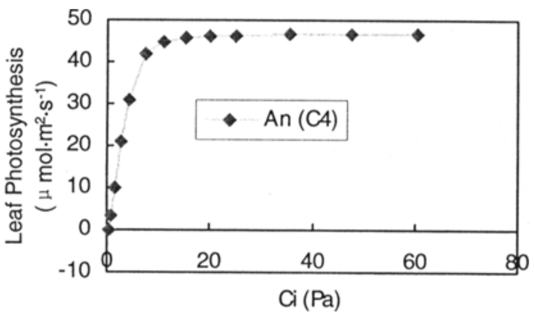

Fig. 4 The relationship between leaf A_n and C_i for C_4 plant

4. Conclusion

Preceding the numerical results present the dependence of leaf photosynthesis rate (An) on Photosynthetic Active Radiation (PAR) curve, the leaf net photosynthesis (A_n) vs. leaf temperature (T_c) response curves in C_3 and C_4 plant, and the leaf net photosynthesis (A_n) vs. intercellar CO_2 concentration (C_i) response curves in C_3 and C_4 plants. The model presented here provides a plausible mechanism for feedbacks of photosynthesis to multiple environmental forcing such as PAR, T_c and C_i. Simulation indicates that the environmental factors have significant influences on the leaf net photosynthetic rate. Whereas, the additional observed experimental studies at the leaf level should be required to test the mechanism proposed here in future work.

To arise from this study, we have demonstrated that the numerical experiments may reveal the main characteristic of plant photosynthesis in C_3 and C_4 plant, and further seem to be used to integrate with the regional climate model and act as land surface process scheme, and better understand the interaction between vegetation and atmosphere.

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